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Species composition, spatial distribution, and the seasonal and interannual dynamics of phytoplankton in brown-water lakes enclosed with reed-belts (Neusiedlersee/Fertő; Austria/Hungary)

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Abstract: Phytoplankton of 12 reed-belt enclosed inner ponds of the large, shallow, alkaline, turbid lake, Neusiedlersee (Austria/Hungary), was studied in the last 13 years. The paper describes the dominant algal groups and their seasonal and interannual quantitative development. Interannual changes are related to those of some physical and chemical variables.

1. A rather rich algal flora can be recorded in the inner lakes. However, most of the species have benthic or periphytic origins. Thus, as in the open lake, the inner lake phytoplankton is characterized by only few dozens of major planktonic species. In inner lakes with small surface areas (1-5 hectares) quantitive contribution of non-planktonic algae (large diatoms, homocytic blue-green and filamentous green algae) can be around 40 %.
2. In small lakes with brown water that is transparent to the bottom, planktonic flagellates (mostly *Cryptomonas* and *Rhodomonas* species) represent the most important group. In bigger lakes in which the water is turbid as a result of stirred up inorganic sediment, non-motile planktonic algae, mostly diatoms, are important. In one of the lakes coccal green algae were the most abundant.
3. Preliminary records show that in transparent, brown-water lakes circadian rhythms of flagellates should not escape consideration in further studies.
4. The seasonal development of phytoplankton was characterized by a mid- or late summer peak biomass. Considerable spring bloom of algae was not observed.
5. The average volume (volumetric biomass [$\mu m^3\ l^{-1}$] divided by the number of individuals) of species peaked in spring or midsummer and reached its seasonal minima during the seasonal peak biomasses. Consequently, the peak biomass in these lakes comprise algae that are easily grazeable for even the smaller, non-selecting zooplankton species.
6. A coccal green/diatom peak developed each year with high degree of regularity in lakes in which the seasonal succession was studied in detail. However, on species level, seasonal development appeared to be quite unpredictable: the peak biomass was provided by different species each year. In this respect the enclosed lakes differ greatly from the open water of Neusiedlersee, in which an extraordinarily low level of seasonality can be observed.
7. The interannually observed increase in phytoplankton peak biomass in both lakes (Haider-Seppl-Poschen-Lacke, Ruster-Poschen) coincided with a drying-out period. This can be well demonstrated by the increasing trend of the conductivity records. PO_4^{3-}-P increased and dissolved N forms (NO_3^- -N and NH_4^+ -N) decreased during the study period. As a consequence, N/P ratio decreased significantly in both lakes. An increase in dissolved oxygen was recorded in one of the lakes. These changes can be considered as consequences of parallel physico-chemical and biological changes. Experimental investigations are necessary for a better understanding of the real causal interconnections. Nevertheless, the results of this study unequivocally prove that the recurrent drying-out periods significantly affect the planktonic habitats and plankton communities in a wetland system.

Kurzfassung: Das Phytoplankton von 12 Lacken, die durch einen Schilfgürtel vom großen, flachen, alkalischen und trüben Neusiedlersee (Österreich/ Ungarn) abgetrennt sind, wurde während der vergangenen 13 Jahre untersucht. Die vorliegende Arbeit beschreibt die dominanten Algengruppen und ihre quantitative Entwicklung sowohl innerhalb eines Jahres als auch über die Jahre. Veränderungen zwischen den einzelnen Jahren wurden den Veränderungen bei einigen physikalischen und chemischen Parametern gegenübergestellt.

1. Für die Schilflacken kann eine recht reichhaltige Algenflora beschrieben werden, jedoch sind die meisten Arten benthischen oder periphytischen Ursprungs. So sind für die Schilflacken, ebenso wie für den offenen See, nur wenige Dutzend planktischer Arten charakteristisch. In Schilflacken mit kleiner Oberfläche (1-5 ha) kann der zahlenmäßige Anteil der nicht-planktischen Arten (große Diatomeen, homozytische Blaualgen und fädige Grünalgen) um 40% betragen.
2. In kleinen Braunwasserlacken mit einer Sichttiefe bis zum Grund bilden planktische Flagellaten (vor allem *Cryptomonas*- und *Rhodomonas*-Arten) die wichtigste Gruppe. In größeren Lacken, in denen das Wasser aufgrund von aufgewirbelten anorganischen Sedimentpartikeln getrübt ist, sind nicht-bewegliche

Planktonalgen, meist Diatomeen, wichtig. In einer der Lacken waren vor allem coccale Grünalgen vertreten.
3. Erste Ergebnisse zeigen, daß für weitere Untersuchungen zirkadiane Rhythmen von Flagellaten in die Betrachtungen einbezogen werden sollten.
4. Charakteristisch für die saisonale Entwicklung des Phytoplanktons war ein Biomassemaximum im Hochsommer oder Spätsommer. Eine ausgeprägte Frühjahrsblüte der Algen konnte nicht beobachtet werden.
5. Das durchschnittliche Volumen der Arten (volumetrische Biomasse [$\mu m^3 l^{-1}$] geteilt durch die Zahl der Individuen) erreichte seinen Höchstwert im Frühjahr bzw. im Hochsommer und seine saisonalen Minima während der saisonalen Biomassemaxima. Folglich setzt sich der Biomassespitzenwert in diesen Lacken aus Algen zusammen, die sogar für kleine, nicht-selektiv fressende Zooplankter leicht aufzunehmen sind.
6. In den Lacken, in denen die saisonale Entwicklung im Detail untersucht wurde, entwickelte sich mit einem hohen Maß an Regelmäßigkeit jedes Jahr ein coccale Grünalgen-/Diatomeen- Maximum. Die saisonale Entwicklung auf Artenebene jedoch schien recht unvorhersehbar zu sein: jedes Jahr sorgten andere Arten für den Biomasse-Peak. In dieser Hinsicht unterschieden sich die vom Schilf umschlossenen Lacken stark vom offenen Wasser des Neusiedlersees, in dem ein außergewöhnlich niedriger Wert an Saisonalität festzustellen ist.
7. Das im Jahresvergleich beobachtete Ansteigen der maximalen Phytoplanktonbiomasse in zwei Lacken (Haider-Seppl-Poschen-Lacke, Ruster-Poschen) verlief zeitgleich mit einer Austrocknungsperiode. Dies kann anhand eines steigenden Trends in der Leitfähigkeit demonstriert werden. Im Untersuchungszeitraum stiegen die Werte für PO_4^{3-}-P an, während die Werte für gelösten Stickstoff (NO_3^--N, NH_4^+-N) geringer wurden. In Folge sank das N/P-Verhältnis in beiden Lacken signifikant. Diese Entwicklungen können als das Ergebnis von parallelen physiko-chemischen und biologischen Veränderungen angesehen werden. Experimentelle Untersuchungen sind nötig, um die Kausalzusammenhänge besser zu verstehen. Nichtsdestoweniger belegen die Ergebnisse dieser Studie eindeutig, daß die wiederholten Austrocknungsperioden in einem Feuchtgebietssystem signifikanten Einfluß auf Planktonhabitate und Planktongesellschaften ausüben.

Introduction

There is an increasing interest in the limnology of continental wetland areas. Neusiedlersee is one of the largest shallow lakes in Central Europe. With its numerous types of habitats ranging from a large open water body across an extensive reed belt to a great number of temporary ditches, the area offers a good opportunity for wetland studies of many kinds.
The surface area of the lake is 300 km^2; it is 35 km long, 8.6 km wide on average, and has a mean depth of 1.3 m (maximum 1.8 m). The theoretical retention time is 3 years. Approximately one third of the lake area is covered by reed swamp.
The mesotrophic lake has a high salt content is alkaline and very turbid. Conductivity ranges in 1000-2300 $\mu S\ cm^{-1}$, alkalinity is 8,0-10,5 mval l^{-1}, and pH is 7,5-10. Secchi transparency in the open water is characteristically about 0.2 m (range: 0.06-0.8 m; higher values occur only under ice).
Neusiedlersee last dried out in 1868 as a consequence of succession of dry years. Since that time an extensive reed belt has developed along the shores, currently covering about one third of the total lake area (Burian & Sieghardt 1979) . However, in the deeper parts of the basin small areas have remained free of reed belt and currently appear as small brown water lakes. They are more characteristic, for geomorphological reasons, and can be found in larger numbers in the southern part of the lake.
According to Takáts's (1984) measurements, the dissolved oxygen content of the inner lakes has usually been lower than that in the lake's open water. Local and moderate summer fish-kills, which were most probably caused by low oxygen concentrations, were observed in Hungarian inner ponds and canals in early 80s (personal observation).
In addition to the fluctuative drying out periods, which operate on a scale of several-years to a decade, the hydrology of the inner lakes is influenced by meteorological conditions. The longitudinal axis of Neusiedlersee is more or less parallel with the most frequent wind directions. Therefore, permanent and strong NW winds result in a 20-25 cm rise in the water level in the southern part of the open water within 8-9 hours. In these cases a 1-2 cm elevation in the water level can be observed in the Herlakni, the largest enclosed lake in the Hungarian section, with a time lag of 13-15 hours (Györke 1986).
Research on the algae of Neusiedlersee has a long history. The first records on the algal flora are from the 1860s (Grunow, 1860, 1862, 1863), and the algal flora has attratced the

interest of many famous algologists ever since (Kusel-Fetzmann 1979). In these studies the presence of an extraordinarily rich algal flora has been described. However, since the open water is inhabited by only a few dozens of characteristic species (Dokulil & Padisák, in press), this high algal biodiversity pertains mostly to the reed-belt area of the lake

Our knowledge of the limnology of the inner ponds of Neusiedlersee is very limited. Takáts (1984) mentioned several aspects of their hydrology and water chemistry. Dinka (1986) studied the elementary composition of the sediment. Algological studies (Padisák 1982, Buczkó 1989; Buczkó & Padisák 1987-88) and other investigations (Lakatos 1989, Farkas et al. 1989) concentrated mostly on the periphyton of the reed at the edges of the inner ponds. Only Padisák's (1981, 1983) pilot studies are available on the phytoplankton of these lakes.

This paper summarizes our present knowledge of the phytoplankton in the small (surface area one to several hectares) open-water lakes enclosed in the Neusiedlersee's extended reed belt. This includes a description of the dominant algal groups and their seasonal and interannual quantitative development. Interannual changes are related to those of some physical and chemical variables.

Description of sites studied

Herlakni (in this paper local names, either the Hungarian or Austrian, are used to specify the different lakes), which has a length of 1200 m and a width of 400 m, is the largest inner lake (Fig. 1). Its water depth is usually 1-1.2 m. Its water is characteristically brownish in colour and moderately turbid as a consequence of stirred up inorganic particles. As in the lake's open water, Secchi transparency rarely exceeds the 20-30 cm. This description also refers to the Haider-Seppl-Poschen-Lacke, the second largest inner lake. Kádler-sarok and Homoki nyelv are similar in many respects; the most important difference between these areas and the other inner lakes is that these have natural connections to the open parts of the lake.

All the other inner lakes are smaller in their size (Table 1), and, except for the Pitner-strand, they have a water depth of 0.7-1.0 m. Their water colour is definitely brown, because of a large amount of dissolved humic material and they are mostly transparent to the bottom. The underwater light climate often permits the development of an epipelic algal carpet characterised by filamentous blue-green algae and large diatoms. Island-like stands of *Phragmites australis* (Cavan) Trin. Steud. occur in all of the inner ponds; at some places stands of *Typha angustifolia* L., *Schoenoplectus litoralis* (Schrad.) Palla and *Najas marina* L. can be found. The Pitner-strand differs from the other lakes in several respects. This lake has an artificial origin; in the early decades of the century it was constructed as an open-air bath with a water depth of about 2 m.

The inner ponds, except for the Ruster-Poschen, belong to the entire zone ('magterület' - 'Kerngebiet') of the Neusiedlersee/Seewinkel National Park.

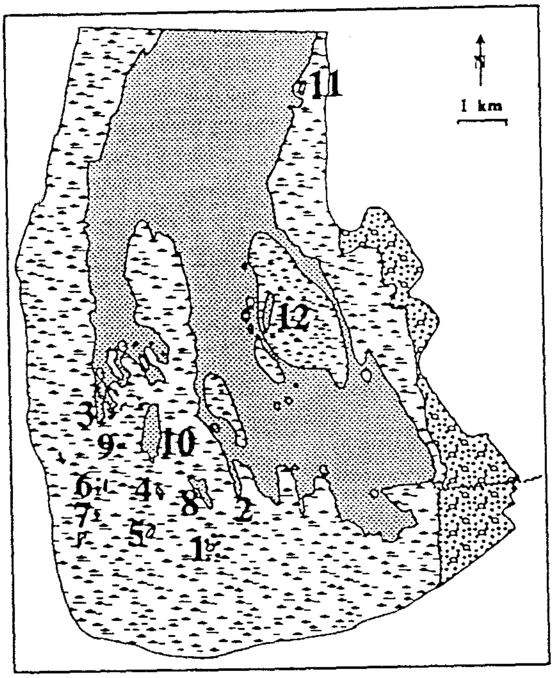

Fig 1: Location of the studied inner ponds within the southeastern reed-belt of Neusiedlersee. 1. Kishatár-tisztás; 2. Homoki-nyelv; 3. Kádler-sarok; 4. Nagyhatár-tisztás; 5. Átjáró-tó; 6. Oberlakni; 7. Pitner-strand; 8: Hidegségi-tó; 9: Kis-Herlakni; 10. Herlakni; 11. Ruster-Poschen; 12. Haider-Seppl-Poschen-Lacke.

Table 1: Some important parameters of the studied inner lakes.

No	Name	origin	connection to the open lake	surface area [ha]	water depth [m]	colour	turbidity	number of phytoplankton samples
1.	Kishatár-tisztás	natural	artificial canal	2	0.8-1	dark-brown	transp. to bottom	1
2.	Homoki nyelv	natural	natural	11	0.8-1	brownish	turbid	1
3.	Kádler-sarok	natural	natural	13	0.8-1	brownish	turbid	1
4.	Nagyhatár-tisztás	natural	artificial canal	3	0.8-1	dark-brown	transp. to bottom	6
5.	Átjáró-tó	natural	artificial canal	3	0.8-1	dark-brown	transp. to bottom	4
6.	Oberlakni	natural	artificial canal	2	0.7-1	dark-brown	transp. to bottom	4
7.	Pitner-strand	aritificial	artificial canal	1	2	dark-brown	transparent	1
8.	Hidegségi-tó	natural	artificial canal	15	0.8-1	dark-brown	transp. to bottom	9
9.	Kis-Herlakni	natural	artificial canal	1.5	0.7-1	dark-brown	transp. to bottom	12
10.	Herlakni	natural	artificial canal	35	1-1.2	brownish	turbid	25
11.	Ruster-Poschen	natural	artificial canal	4	0.9-1.1	brown	transparent	70
12.	Haider-Seppl-Poschen-Lacke	natural	artificial canal	10	0.9-1.1	brownish	turbid	97

Material and methods

The phytoplankton in 12 inner lakes has been studied in the last 13 years. Samples in the Hungarian part of the lake were taken with a glass-tube sampler. In the Austrian inner ponds (Haider-Seppl-Poschen-Lacke, Ruster-Poschen) large-volume surface samples were taken. It should be noted at this point that sampling can be easily prevented in the inner ponds of the lake, because the canals that connect them to the open water are frequently impenetrable in dry seasons of particular years and during dry years in general. This was the main cause of the scarce sampling in the southern inner ponds (cf. Padisák 1983).

The phytoplankton was counted under an inverted microscope. A minimum of 400 cells/sample were counted (counting error or ± 10 %). Biomass was estimated by geometrical approximations. In this paper biomass records were considered for the description of quantitative phytoplankton changes.

Several water chemical records are used in this paper. These records derive from the archives of the Biologische Station Illmitz. All the parameters were measured according to widely accepted international standards from samples parallel to phytoplankton samples.

Results and discussion

1. Species composition

Many species of algae can be found in the plankton samples taken in the inner ponds. However, most of these species have epipelic or epiphytic origin. Table 2 summarizes the most frequent species of algae, and Fig. 2 shows the biomasses of the main algal groups.

In some cases homocytic blue-green algae, like *Oscillatoria* and *Spirulina* were found in large numbers in the smaller inner lakes. Heterocytic blue green algae, however, were very rarely been observed in the plankton In the summer of 1990 *Anabaenopsis elenkinii* V. Miller bloomed in the canal at the Biologische Station Illmitz, one single filament of this species was found in Haider-Seppl-Poschen-Lacke in a 1992 late-autumn sample. Kusel-Fetzmenn (personal communication) also found the species in Neusiedlersee samples. Since the late seventies *Microcystis spp.* have formed many local water blooms along the edge of the lake's open water (Hofbauer, 1984). Such a bloom is reflected in the records of the Kádler sarok.

Table 2: The most important species (genera) of algae in the inner ponds (1. Kishatár-tisztás; 2. Homokinyelv; 3. Kádler-sarok; 4. Nagyhatár-tisztás; 5. Átjáró-tó; 6. Oberlakni; 7. Pitner-strand; 8: Hidegségi-tó; 9: Kis-Herlakni; 10. Herlakni; 11. Ruster-Poschen; 12. Haider-Seppl-Poschen-Lacke) of Neusiedlersee. Numbers indicate the percentage contributions to total biomass taking the avarage of all the available samples into consideration.

species/locality	1	2	3	4	5	6	7	8	9	10	11	12
Microcystis spp.			41									
Oscillatoria spp.	18				10							
Spirulina spp.	15							5	5			
Euglena spp.	10	8	9	5								20
Cryptomonas spp.	21	32	28	53	22	72	48	38	36	14	19	10
Rhodomonas spp.		19	8	10		6		11	8	12	14	6
Peridinium sp.					17							
Campylodiscus clypeus										34		
Cymbella spp.					10							
Fragilaria spp.		6						25	16		12	
Nitzschia reversa												8
small Nitzschia spp.				8		5						5
Synedra ulna				5								
Chaetoceros muellerii												8
Cyclotella meneghiniana		5										
small unicellular centrics												8
Chlamydomonas sp.	6						41					
chlorelloid unicells											12	
Ankistrodesmus minutissimus		5										
Koliella sp.		7										
Monoraphidium contortum							5					
others	30	24	14	19	41	17	6	21	35	40	43	35

In the summer of 1988 a large number of pseudofilaments of *Romeria sp.* (most resemble *Romeria crassa* Hindák, Hindák 1988) appeared in the plankton of Haider-Seppl-Poschen-Lacke. Since then the species appears each year, although in a much smaller amount.

Species of Euglenophyta were found in both largest species number and amount in the Haider-Seppl-Poschen-Lacke. A smaller and a bigger form of *Euglena oxyuris* Schmarda and *E. acus* Ehr. predominated.

Cryptophytes are the most characteristic algae in the inner ponds, especially in those which have a small surface area and/or shallow depth. *Cryptomonas spp.* are represented by *C. ovata* Ehr. and *C. erosa* Ehr. and sometimes by a bigger, unidentified *Cryptomonas sp.* (*C. rostrata*?). The dominant *Rhodomonas* can most probably be identified as *R. lacustris Pascher & Ruttner*, *R. minuta* Skuja or *R. minuta var. nannoplanktica Skuja*.

Dinoflagellates were not found in large amounts except for unidentified forms once in the Átjáró tó and once in the Ruster-Poschen. However, it should be mentioned that winter-dinoflagellates regularly occur in a small amounts in the inner lakes.

Diatoms, which represent the main group of the plankton in the open lake (Padisák & Dokulil 1992) are numerically less important in inner lakes. Planktonic diatoms appear in larger amounts only in the larger enclosed lakes: in Herlakni *Campylodiscus clypeus* Ehr. and sometimes *Cyclotella meneghiniana* Kütz. were important. A very characteristic diatom peak developed in the Haider-Seppl-Poschen-Lacke each year. The species composition of this peak, however, was not constant: in some years one or several species of unidentified small centrics and *Chaetoceros muellerii* Lemm. and more recently small *Nitzschia spp.*, especially *N. reversa* W. Smith dominated. We tried to determine the 1988 small centric peak by transmission and scanning electron microscopy, but by the time (approx. one year) these studies were to be made, the diatom frustules disappeared (dissolved?) from the Lugol-fixed samples.

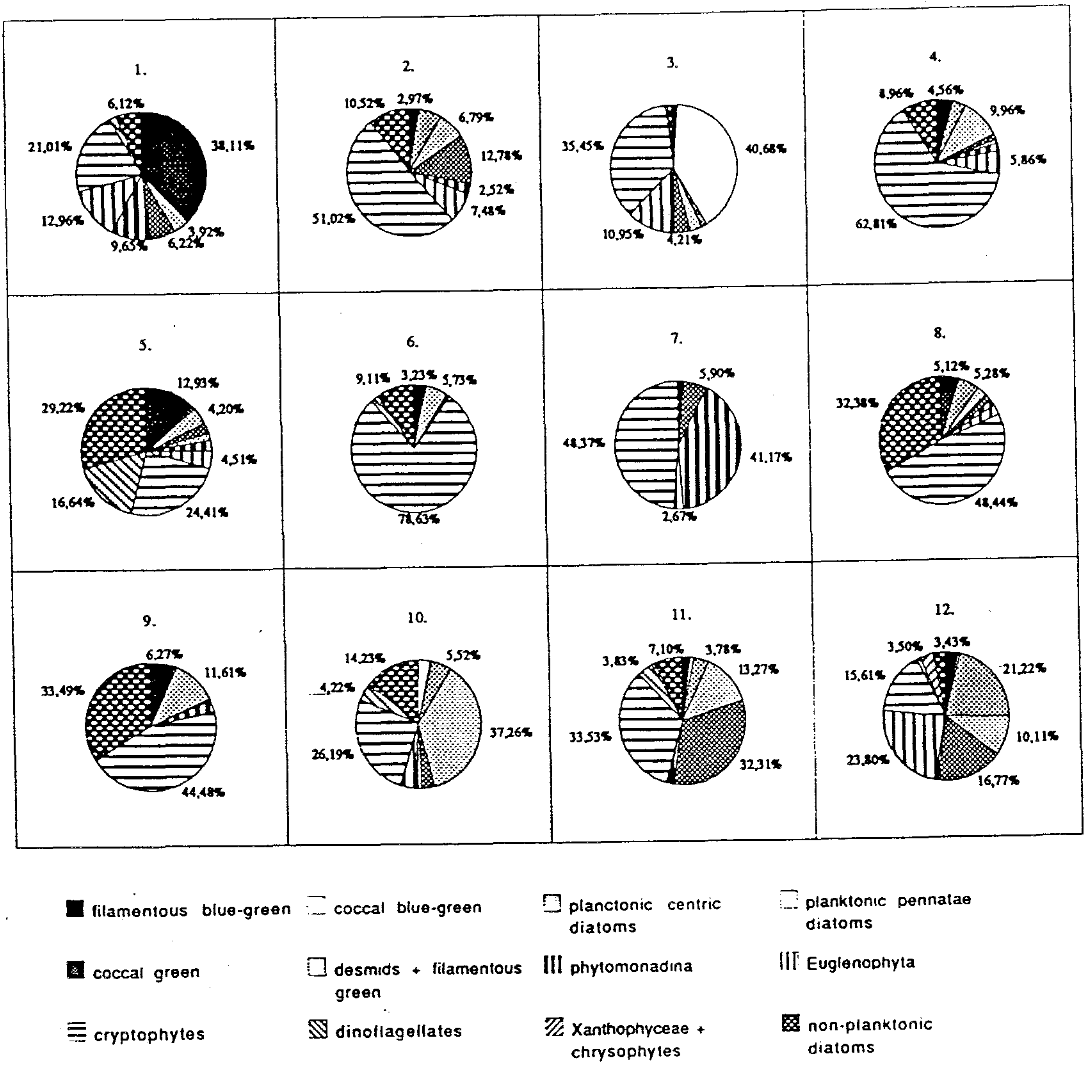

Fig. 2: Contribution of the main algal groups to total biomass (average of all the available samples) in the inner ponds (1. Kishatár-tisztás; 2. Homoki-nyelv; 3. Kádler-sarok; 4. Nagyhatár-tisztás; 5. Átjáró-tó; 6. Oberlakni; 7. Pitner-strand; 8: Hidegségi-tó; 9: Kis-Herlakni; 10. Herlakni; 11. Ruster-Poschen; 12. Haider-Seppl-Poschen-Lacke) of Neusiedlersee.

Chlorophyta are usually negligible in the inner ponds. In the larger ponds those species can be found which are characteristic of the planktonic green-algal flora of the open lake. The only significant exception is the Ruster-Poschen. In this lake phytomonads provided a small, but rather consequent late-winter or early-spring maximum, and Chlorococcales exhibited a very definite summer peak. In the latter peak, *Tetraedron minimum* (A. Br.) Hansgirg *T. caudatum* (Corda) Hansgirg, *Crucigenia quadrata* Morren, *C. tetrapedia* (Kirchn.) W. & G. S. West, *Planctosphaeria gelatinisa* G. M. Smith, *Oocystis spp.* and *Scenedesmus spp.* were identifiable. However, spherical or ellipsoid monocells contributed mainly to the summer peak biomass. These monocells were mostly unidentifiable, but sometimes their resemblance to the cells of the above listed species was unequivocal. Unicells of *Crucigenia quadrata* and monodesmoid *Scenedesmus* were frequently recognizable. No comparable amount of such unicells were seen by the author in other natural shallow waters.

On some kind of life-form basis (Fig. 3), planktonic flagellates are the most characteristic group of algae in the inner ponds; they usually represent more than 50% of the total biomass. Non-planktonic algae form an important group in the shallower inner lakes in the Hungarian part. Non-motile planktonic species reach a significant contribution in the bigger, turbid lakes. Ruster-Poschen is the only inner lake in which this group plays an important role despite the fact its water is rather brown and transparent.

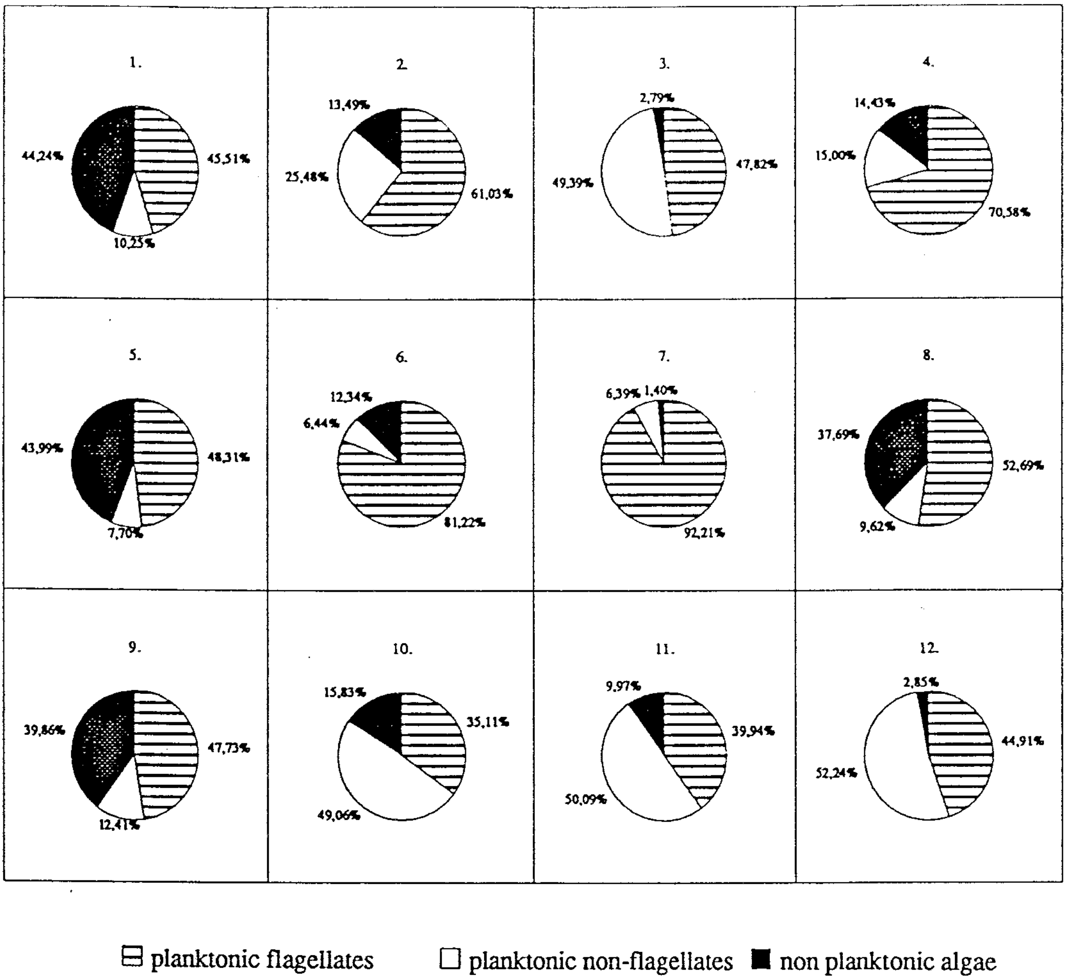

Fig. 3: Contribution of planktonic flagellates, planktonic non-flagellates and non-planktonic algae to total biomass (average of all the available samples) in the inner ponds (1. Kishatár-tisztás; 2. Homoki-nyelv; 3. Kádler-sarok; 4. Nagyhatár-tisztás; 5. Átjáró-tó; 6. Oberlakni; 7. Pitner-strand; 8: Hidegségi-tó; 9: Kis-Herlakni; 10. Herlakni; 11. Ruster-Poschen; 12. Haider-Seppl-Poschen-Lacke) of Neusiedlersee.

2. Vertical distribution

On 13 August 1980 plankton samples were taken from different depths in Herlakni and in Hidegségi-tó. The sampling in the two lakes was conducted late in the morning and with only a half an hour difference. In Herlakni flagellates (Euglenophyta spp., *Cryptomonas spp., Rhodomonas spp.)* avoided both the surface and the above bottom layer; *Microcystis spp.* peaked at the surface. In the transparent Hidegségi-tó (rather brown water colour) the dominant species preferred the surface-layer of the water. Vertical distribution of the ciliates (species composition is unknown) in both lakes is also given (Figs. 4, 5). The preliminary study described here calls attention to the fact that vertical distribution must be considered in further studies.

3.Seasonal development of phytoplankton

In 1982, when the seasonal development of phytoplankton was studied in the Hungarian enclosed lakes with roughly a monthly frequency, a high degree of both spatial and temporal variability was found (Padisák 1983). However, it was impossible to judge wheather the observed variability was an inherent feature of this phytoplankton or merely a consequence of the rare sampling. In the Ruster-Poschen and the Haider-Seppl-Poschen-Lacke, the four to five years of study with weekly-biweekly sampling provided a rather regular, though different, seasonal development.

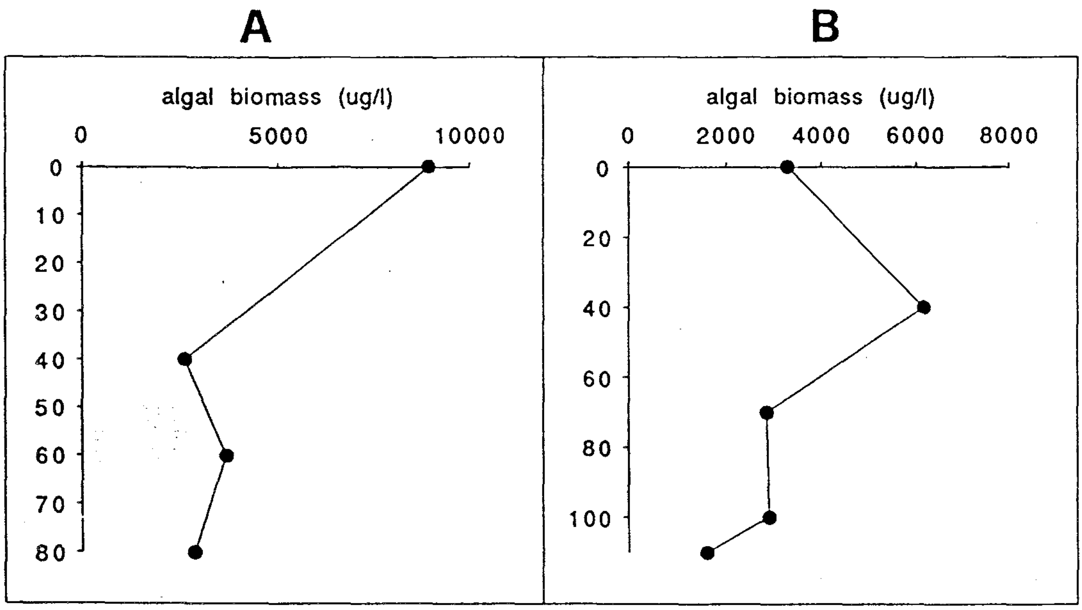

Fig. 4: Vertical distribution of phytoplankton biomass (µg freshweight l^{-1}) in Hidegségi-tó (A) and in Herlakni (B) on 13 August, 1980.

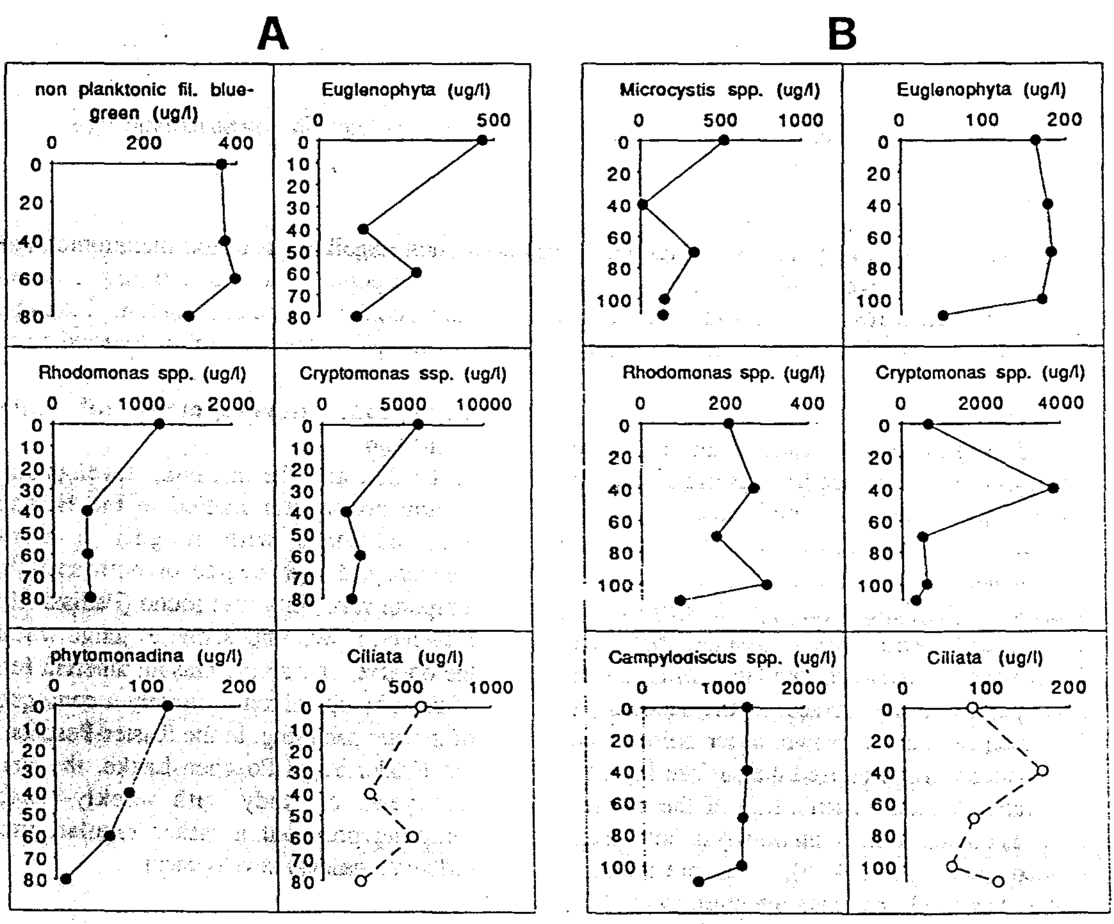

Fig. 5: Vertical distribution of some phytoplankton species and Ciliates (biomass; µg freshweight l^{-1}) in Hidegségi-tó (A) and in Herlakni (B) on 13 August, 1980.

Haider-Seppl-Poschen-Lacke. A rather regular latesummer - autumn maximum biomass developed in each year of the investigation (Fig. 6). Except for the year 1987, when the studies began, the peak biomass was between 12,000 and 20,000 µg l^{-1}. The lowest biomasses, which did not exceed the 2,000 µg l^{-1}, were found in early spring. The average volume of phytoplankton (the volumetric biomass [μm^3 l^{-1}] divided by the number of individuals) peaked in early or midsummer before the biomass peak (Fig. 7). This observation does not accord with findings in many lakes (e. g. Sommer et al., 1986) in which a parallel relation has occurred: the late-summer biomass maximum was provided by the algae with the largest cell sizes.

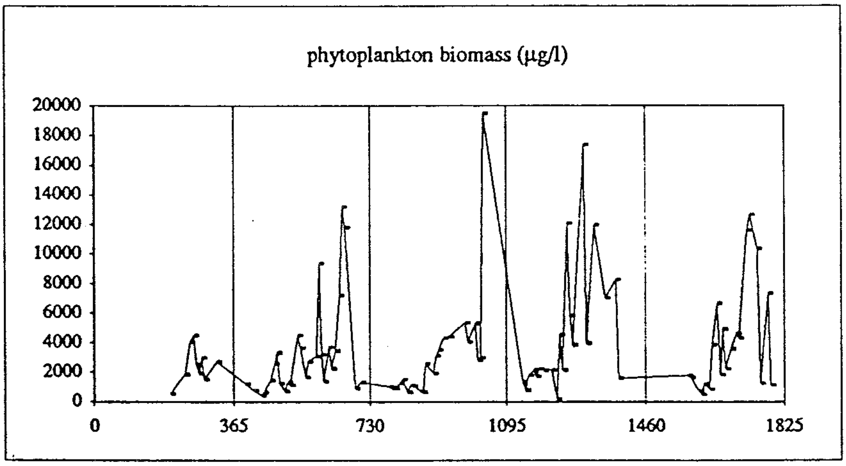

Fig. 6: Phytoplankton biomass (µg freshweight l^{-1}) in the Haider-Seppl-Poschen-Lacke between 1987 and 1991. Days are numbered consecutively; 1 correspond to 1 January, 1987). Vertical gridlines separate years.

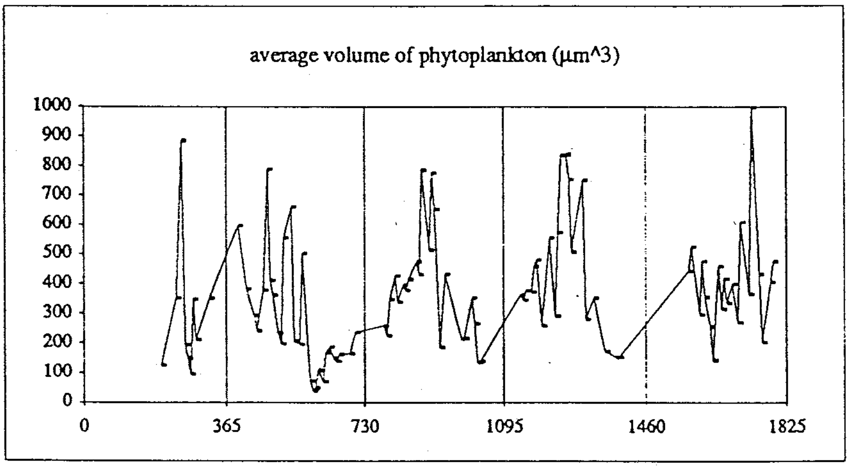

Fig. 7: Average volume (μm^3) of phytoplankton cells in the Haider-Seppl-Poschen-Lacke between 1987 and 1991. Days are numbered consecutively; 1 correspond to 1 January, 1987). Vertical gridlines separate years.

Blue-green algae are usually insignificant in this lake. The year 1988 was an exception: a dense population of *Romeria* developed, and its biomass peaked at almost 5,000 $\mu g\ l^{-1}$ (Fig. 8). This species also occurred in subsequent years in small amounts. Euglenophyta form a dense population always in the warm season; the peak biomass ranged between 2,000 and 9,000 $\mu g\ l^{-1}$. Dinoflagellates also reached their maximal biomass in the warm season, although their quantitiy was not as significant as that of other algal groups. Chrysophytes reached a biomass of 4,000 $\mu g\ l^{-1}$ only once, in late 1989. This biomass peak was provided by an unidentified, *Chrysidalis*-like, small, spherical chrysoflagellate species with a diameter of 3-4 µm. Cryptophytes can reach a high biomass in almost any season except winter. Diatoms were the principal contributors to the late summer - autumn biomass peak. Only a small increase in their biomass was found in 1987, while in subsequent years they increased significantly. In 1988 and 1989 the peak biomass was provided by centric diatoms, *Chaetoceros muellerii* and *Cyclotella meneghiniana* among several small-sized unidentified species, while pennatae diatoms (most notably *Nitzschia reversa* and other *Nitzschia spp.* with smaller cell-sizes) became increasingly abundant in the following years. The appearance of non-planktonic diatoms did not show definite seasonality and their quantity is negligible as compared to the planktonic ones.

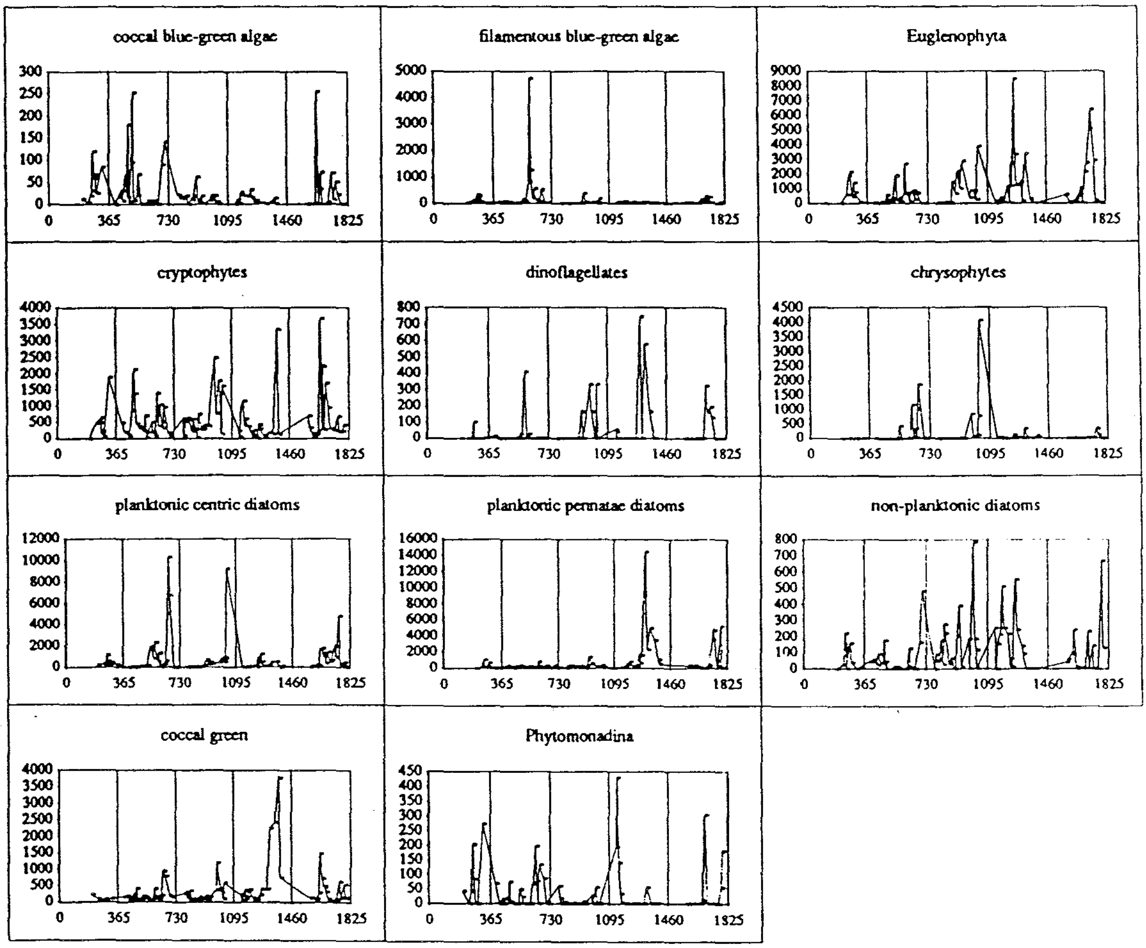

Fig. 8: Biomass (μg freshweight l^{-1}) of the main algal groups in the Haider-Seppl-Poschen-Lacke between 1987 and 1991. Days are numbered consecutively; 1 correspond to 1 January, 1987. Vertical gridlines separate years.

Coccal green algae did not reach large biomasses. Their species composition is similar to that in the open lake: *Crucigenia quadrata*, *Oocystis lacustris* Chod., *O. solitaria* Wittr., *Elakatothrix lacustris* Kors., *Lobocystis dichotoma* Thompson, *Monoraphidium contortum* (Thur.) Kom.-Legn., *M. pseudobraunii* (Belch. & Swale) Heynig, *M. minutum* (Näg.) Kom.-Legn. *Koliella sp.*, *Pediastrum duplex* Meyen and *Planctosphaeria gelatinosa* were the most frequent.

Ruster-Poschen. The Ruster-Poschen, like the Haider-Seppl-Poschen-Lacke, had only one large biomass peak (9,000-14,000 $\mu g\ l^{-1}$) each year (Fig. 9). This peak, however, occurred in mid-summer, a bit earlier than that in the other lake. In 1989 and 1990 a slight spring biomass increase, up to 5,000-7,000 $\mu g\ l^{-1}$, was observable. Phytoplankton biomass and the average volume of algae showed a clear inverse relationship: the peak biomass was given by cells of the smallest dimensions (Fig. 10). Blue-green algae and euglenophytes never occurred in large amounts in this lake, and their appearance did not show definite seasonality (Fig. 11). *Rhodomonas* and especially *Cryptomonas spp.* were found in large amounts (1,000-3,000 $\mu g\ l^{-1}$) almost invariably in any season. Dinoflagellates usually occurred in small amounts; once, in the summer of 1990, an unidentified form reached a peak biomass of 10,000 $\mu g\ l^{-1}$. Chrysophytes were represented by a *Chrysidalis* -like small flagellate (diameter: 3-4 μm). It reached a peak biomass of 430 $\mu g\ l^{-1}$ in February 1990. *Chaetoceros muellerii* was the most characteristic among planktonic centric diatoms, and peaked regularly in summer. The highest biomass was recorded as almost 1,000 $\mu g\ l^{-1}$ in the summer of 1990. *Fragilaria construens* (Ehr.) Grun., the most abundant diatom in the lakes's open water during the years of these investigations, was the most numerous planktonic pennatae diatom with maximal biomasses of about 1,000 $\mu g\ l^{-1}$ in the warm season. Non-planktonic diatoms characteristically appeared in larger amount (1,000-2,000 $\mu g\ l^{-1}$) in the spring samples. Planktonic chlorophytes were found to be the most important group in this lake. The group Phytomonadina (*Chlamydomonas spp.*, including *Ch. reinhardtii* Dang., *Carteria sp.*) had a small (about 300 $\mu g\ l^{-1}$), but rather regular peak in the early spring. Coccal green algae provided the absolute peak biomass (7,000-11,000 $\mu g\ l^{-1}$) midsummers.

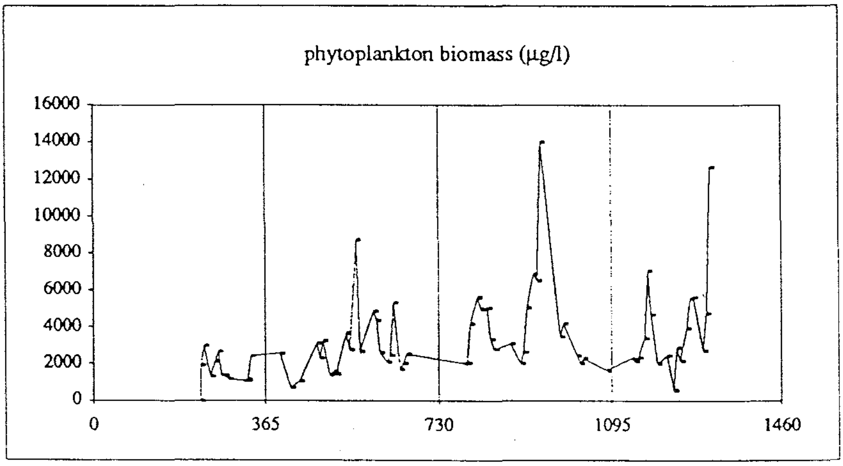

Fig. 9: Phytoplankton biomass (μg freshweight l^{-1}) in the Ruster-Poschen between 1987 and 1990. Days are numbered consecutively; 1 correspond to 1 January, 1987). Vertical gridlines separate years.

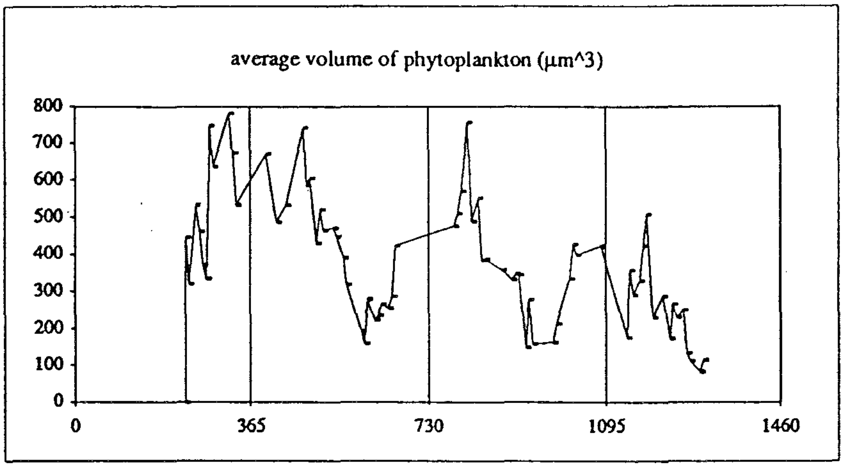

Fig. 10: Average volume (μm^3) of phytoplankton cells in the in the Ruster-Poschen between 1987 and 1990. Days are numbered consecutively; 1 correspond to 1 January, 1987). Vertical gridlines separate years.

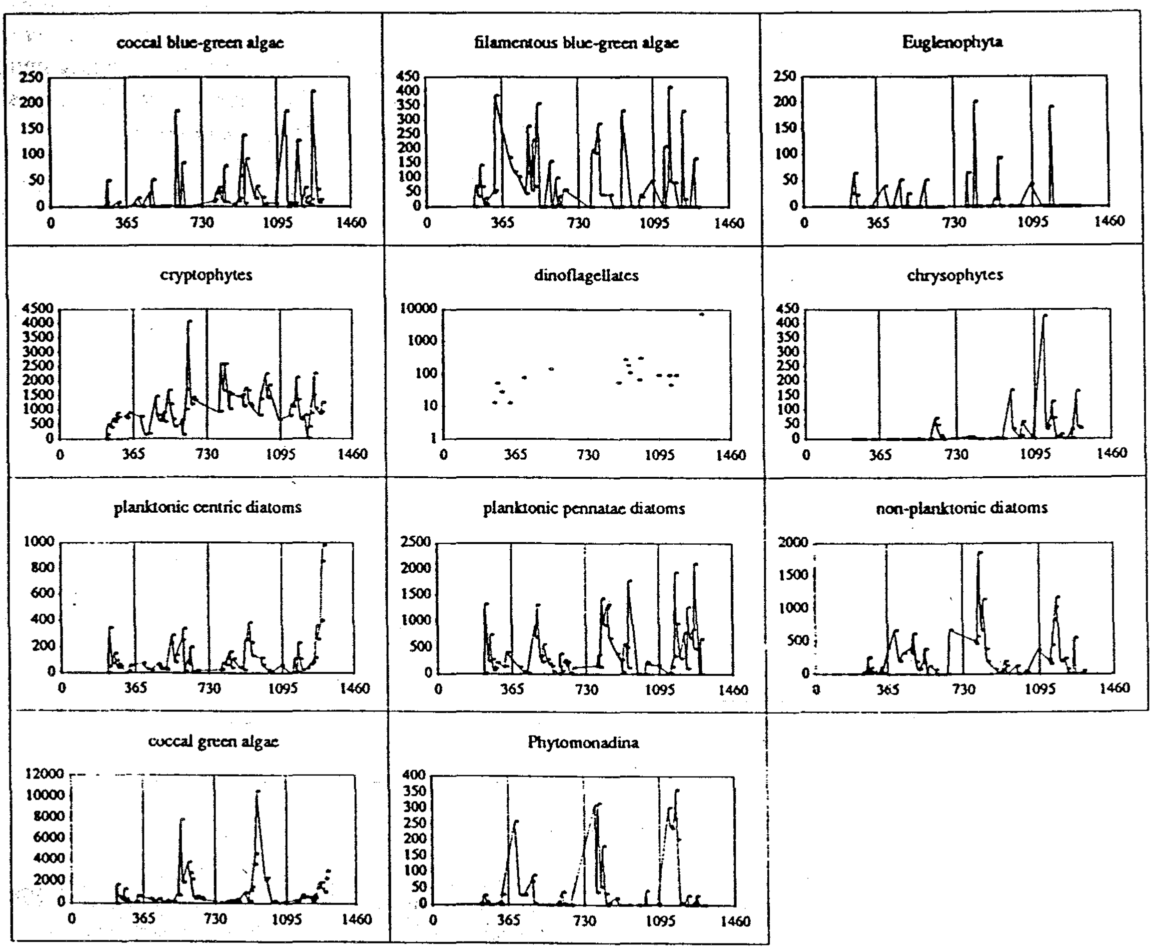

Fig. 11: Biomass (µg freshweight l^{-1}) of the main algal groups in the Ruster-Poschen between 1987 and 1990. Days are numbered consecutively; 1 correspond to 1 January, 1987). Note: logarithmic scale for dinoflagellates. Vertical gridlines separate years.

4. Comparision with some physical parameters

Simultaneously with phytoplankton samples, several major background variables were also measured.

Most of the study period (1987-1990) coincided with successive dry years. As a consequence of low annual precipitation, the water level of the lake receded. In shallow, alkaline lakes, changes in conductivity has been an important indicator of drying out periods. Conductivity in such lakes has a definite seasonality: the highest values occur invarably before the autumn rainy period, while winter and early spring months are characterized by the lowest records. This seasonality is well reflected in both lakes (Fig. 12, 13). Moreover, there is an overall increasing tendency. The increase in conductivity was so pronounced in the Ruster-Poschen that the lowest winter-records in 1989/90 were in the same range with the highest summer records in 1987.

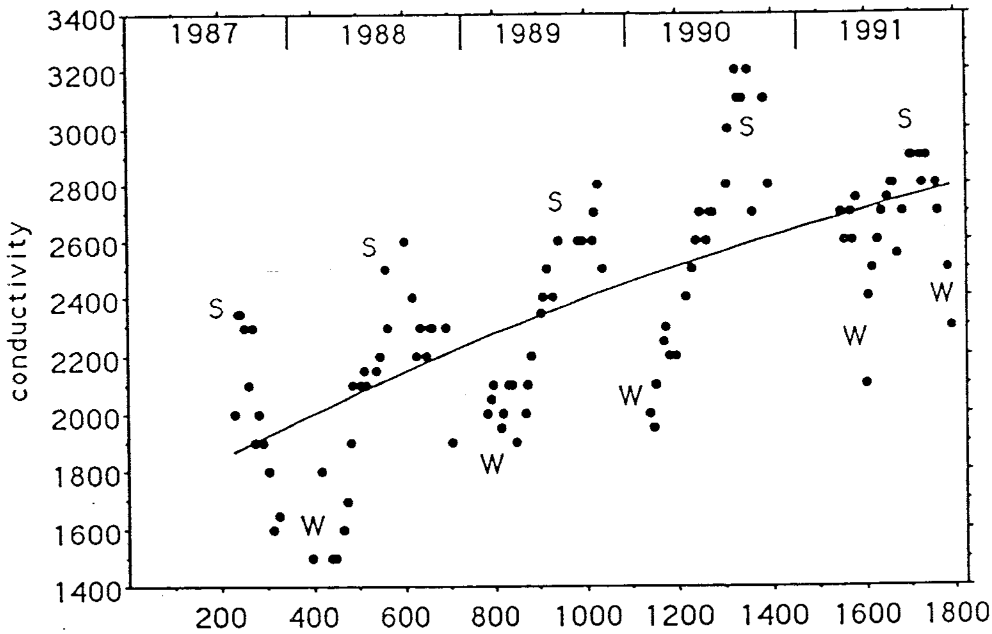

Fig. 12: Conductivity ($\mu S\ cm^{-1}$) in the Haider-Seppl-Poschen-Lacke between 1987 and 1991. Days are numbered consecutively; 1 correspond to 1 January, 1987). *S* indicate the summer, and *W* the winter records. An orthogonal polinom was fitted on the data to indicate the trend of change.

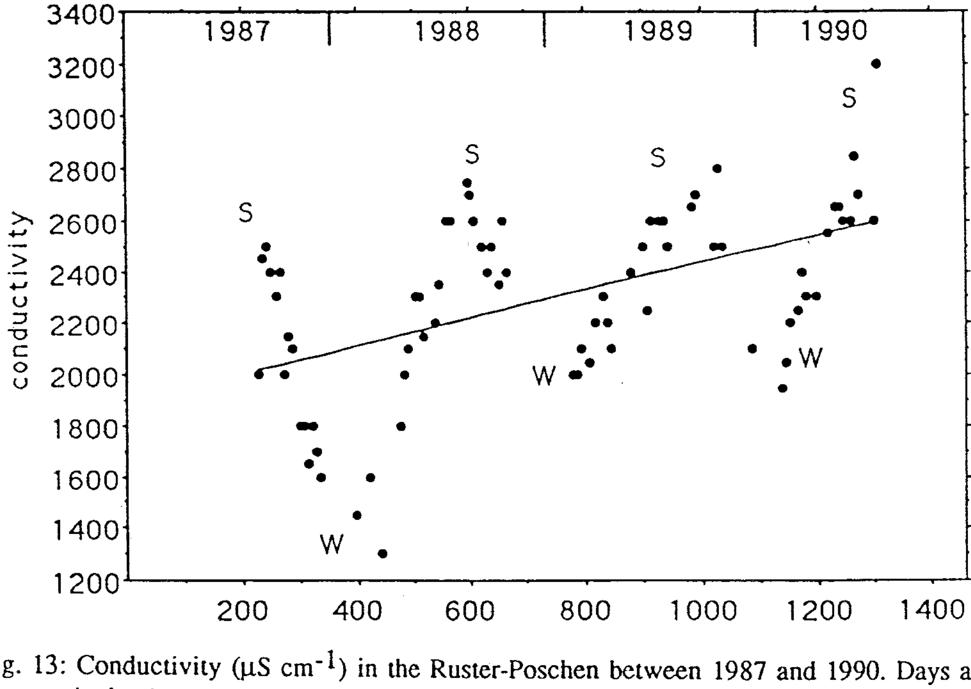

Fig. 13: Conductivity ($\mu S\ cm^{-1}$) in the Ruster-Poschen between 1987 and 1990. Days are numbered consecutively; 1 correspond to 1 January, 1987). *S* indicate the summer, and *W* the winter records. An orthogonal polinom was fitted on the data to indicate the trend of change.

Dissolved nitrogen forms (NO_3^- -N and NH_4^+ -N) decreased in the last 4-5 years in both lakes (Fig. 14). The decrease was more pronounced in the Ruster-Poschen. Despite nitrogen, PO_4^{3-} -P increased gradually Fig. 14); the trend was stronger in the Haider-Seppl-Poschen-Lacke. As a consequence of the above outlined trends in changes of the most important nutrients for phytoplankton, the dissolved N/P ratio decreased significantly in both lakes at practically the same rate (Fig. 14). It is customary (see Padisák 1985 and the references cited there) to suppose N-limitation if $N/P < 7$, P-limitation if $N/P > 20$ and a combined N and P limitation if the values are between 7 and 20. In these terms there was a shift from P to combined N and P limitation in the Haider-Seppl-Poschen-Lacke, although limitation by light (stirred-up inorganic particles) can play an important role in this lake.

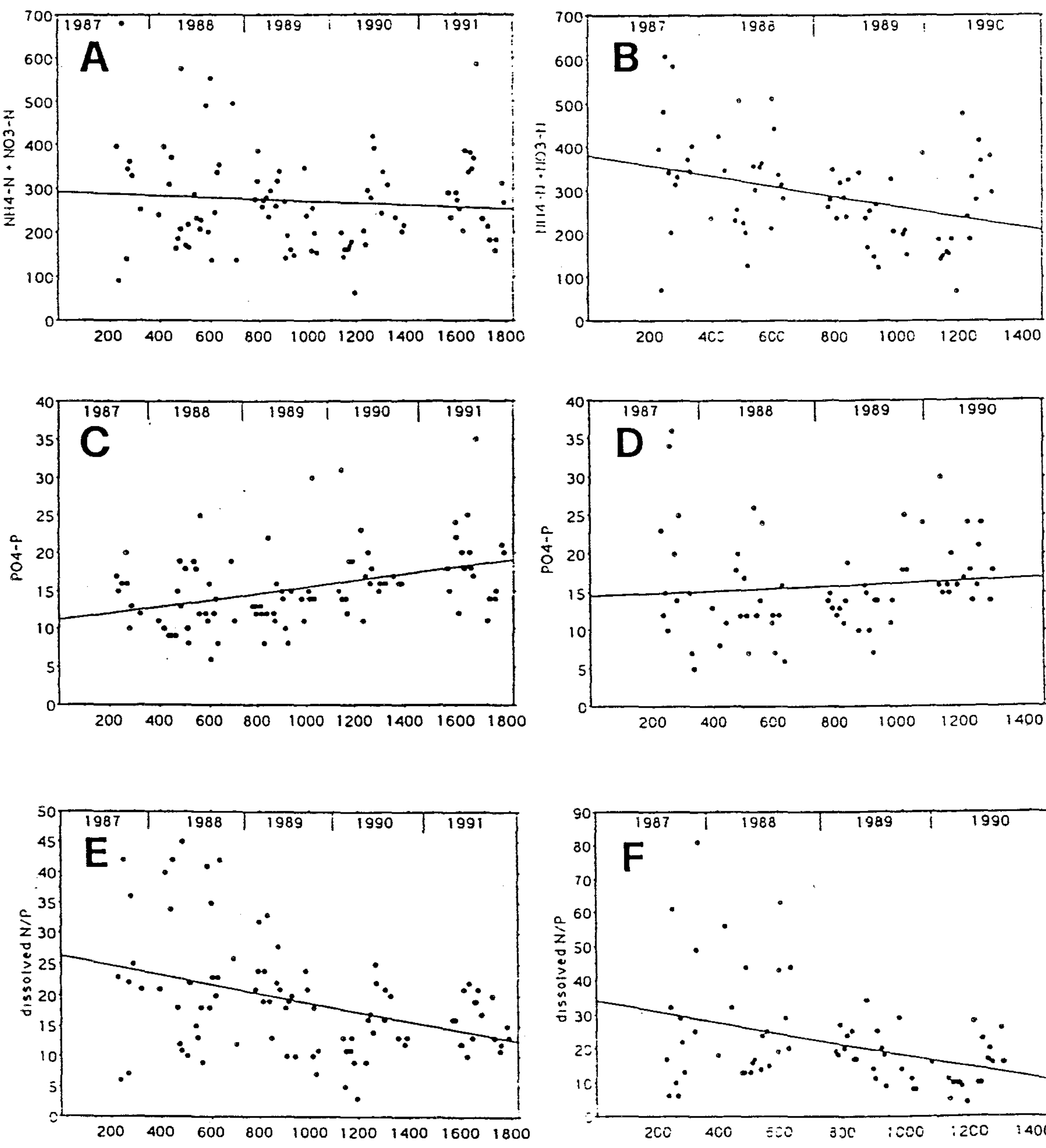

Fig. 14: Concentration of PO_4-P (A, B; µg l^{-1}), NH_4-N + NO_3-N (C, D; µg l^{-1}) and the N/P ratio of the dissolved fraction (E, F) in the Haider-Seppl-Poschen-Lacke (A, C, E; 1987-1991) and in the Ruster-Poschen (B, D, F; 1987-1990). An orthogonal polinom was fitted on the data to indicate the trend of change. Days are numbered consecutively; 1 correspond to 1 January, 1987).

In the Ruster-Poschen the N/P values were initially lower, therefore by 1990 data that suggest N-limitation were recorded. The increasing records on the presence of the heterocytic *Anabaenopsis elenkinii* may indicate the same. The above N/P ratio based limitation concept can be criticized from different viewpoints (those are rather the absolute values which matter than the ratios; different species of phytoplankton have rather different nutrient demand and strategies to obtain nutrients, etc.). It should be noted, moreover, that changes in nutrient ratios can well be consequences and not causes of changes in algal biomass.

While dissolved oxygen content did not show interannual changes in the Haider-Seppl-Poschen-Lacke, it exhibited a definite increasing trend in the Ruster-Poschen (Fig. 15). Considering that summer minima in 1987 and 1988 occurred around or even below 5 mg l^{-1} while later minimal records were found to be regularly above 5 mg l^{-1}, the observed increase means that the changes occurred towards the establishment of a continuously oxygen saturated environment, which can be important for all animals from zooplankton to fish. The increase in oxygen content may be a consequence of either physical (the water depth therefore the water volume decreased while the surface of the lake did not) or biological (the algal biomass increased; Fig. 16) processes, or both. Meanwhile, the differences in oxygen changes in the two lakes of different size suggest that the physical processes can play a more important role in this respect.

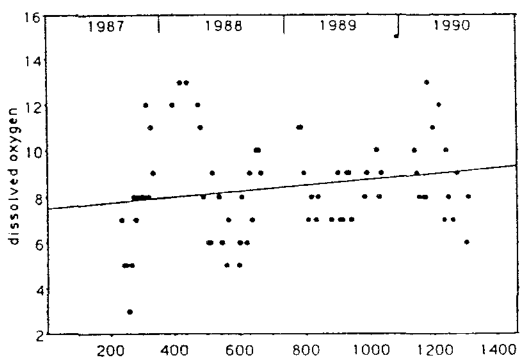

Fig. 15: Dissolved oxygen concentration (mg l^{-1}) in the Ruster-Poschen between 1987 and 1990. An orthogonal polinom was fitted on the data to indicate the trend of change. Days are numbered consecutively; 1 correspond to 1 January, 1987).

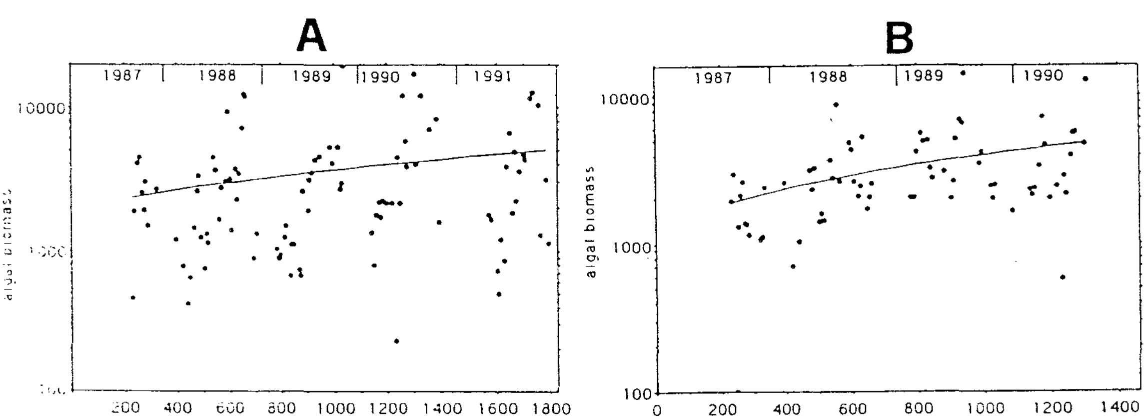

Fig. 16: Algal biomass (µg freshweight l^{-1}; logarythmic scales) in the Haider-Seppl-Poschen-Lacke (A; 1987-1991) and in the Ruster-Poschen(B; 1987-1990). An orthogonal polinom was fitted on the data to indicate the trend of change. Days are numbered consecutively; 1 correspond to 1 January, 1987.

5. Summarizing conclusions

1. A rather rich algal flora can be recorded in phytoplankton samples taken from the reed-belt enclosed inner lakes in Neusiedlersee. However, most of the species have epipelic or periphytic origins. Thus, as in the open lake, the inner lake phytoplankton is characterized by only few dozens of major planktonic species. In inner lakes with small surface areas (1-5 hectares) quantitive contribution of non-planktonic algae (large diatoms, homocytic blue-green and filamentous green algae) can be around 40 %.
2. There is a clear relationship between the taxonomic/life-form composition of phytoplankton and the size/colour of the inner lakes. In small lakes with brown water that is transparent to the bottom, planktonic flagellates (mostly *Cryptomonas* and *Rhodomonas* species) represent the most important group. In bigger lakes in which the water is turbid as a result of stirred up inorganic sediment, non-motile planktonic algae, mostly diatoms, are important. The only exception is the Ruster-Poschen, in which, despite its brown water colour and considerable transparency, non-motile coccal green algae made the greatest contribution to total biomass.
3. Vertical stratification can be considerable mostly in transparent, brown-water lakes. This aspect of the ecology of phytoplankton as well as the possibly important circadian rhythms of flagellates should not escape consideration in further studies. Preliminary records show that the importance of stratification pertains to planktonic ciliates as well.
4. Changes in phytoplankton biomass showed definite seasonality in both inner lakes where it was studied regularly over several years. The seasonal development of phytoplankton was characterized by a mid- or late summer peak biomass. Considerable spring blooms of algae were not observed. The consequent lack of the spring bloom is supported by the scarce data from the southern inner lakes (Padisák, 1981, 1983).
5. The average volume (volumetric biomass [$\mu m^3 l^{-1}$] divided by the number of individuals) of species peaked in spring or midsummer in both lakes; and reached its seasonal minima during the seasonal peak biomasses the average volume. Consequently, the peak biomasses in these lakes comprise algae that are easily grazeable for even the smaller, non-selecting zooplankton species.
6. The seasonal dynamics of the phytoplankton assemblage were found to be quite distinct in different lakes: the summer biomass peak was consisted of coccal green algae in one of the lakes, while in the other diatoms were very dense. This coccal green/diatom peak developed each year with high degree of regularity. In this respect the enclosed lakes differ greatly from the open water of Neusiedlersee, in which an extraordinarily low level of seasonality can be observed (Dokulil & Padisák, in press).
7. Despite that which is observed in most of the other natural lakes in which phytoplankton dynamics are characterized by annually recurrent sequence of dominant species, seasonal development appeared to be quite unpredictable: the peak biomass was provided by different species each year.
8. The interannually observed increase in phytoplankton peak biomass in both lakes coincided with a drying-out period. This can be well demonstrated by the increasing trend of the conductivity records. PO_4^{3-}-P increased and dissolved N forms (NO_3^- -N and NH_4^+ -N) decreased during the study period. As a consequence, N/P ratio decreased significantly in both lakes. An increase in dissolved oxygen was recorded in one of the lakes. These changes can be considered as consequences of parallel physico-chemical and biological changes. Experimental investigations are necessary for a better understanding of the real causal interconnections. Nevertheless, the results of this study unequivocally prove that the recurrent drying-out periods significantly affect the planktonic habitats in a wetland system.

Acknowledgements

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